Temporal and spatial patterns in emergence and early survival of perennial plants in the Sonoran Desert

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Abstract

Seedling emergence and survival of 15 perennial species were studied for six years in a 557-m^2 permanent plot at Tumamoc Hill, Arizona, USA, an ungrazed site in the northern Sonoran Desert. The minimum rain required for germination and emergence ranged from 17.5 to 35.6 mm. Few species emerged in every year of the study. First-year survival averaged across all 15 species was 3.7%; only 0.1% of seedlings lived as long as four years. The odds of survival in the first year improved with increased rain. About three times as many seedlings died from predation as desiccation. In 2-m^2 subplots, mortality of three woody species in the first 30 days after emergence appeared to be independent of seedling density. Short-, moderate-, and long-lived species displayed distinct survival strategies. Long-lived species compensated for generally poor seedling survival by frequent germination and emergence. Moderate-lived species exhibited highly episodic germination and emergence, a potentially risky behavior that might have been offset to some extent by relatively good long-term survival. Short-lived species had the highest seedling survival. Because these species can bloom in their first year, good early survival meant that some individuals were able to reproduce before they died.

Introduction

The episodic nature of plant establishment in the arid southwestern United States has been demonstrated repeatedly. High seed and seedling mortality has been ascribed to several forms of interannual variability: (1) in climate, especially rainfall (Shreve 1917; Sherbrooke 1977; Jordan and Nobel 1981; Bowers and Pierson 2001); (2) in consumption of seeds and seedlings by herbivores (Steenbergh and Lowe 1977; Boyd and Brum 1983a; McAuliffe 1986, 1990; Bowers and Pierson 2001); and (3) in flower and seed production (Shreve 1917; Boyd and Brum 1983b; Sherbrooke 1977, 1989). Other factors besides seed and seedling mortality that influence plant establishment include spatial patterns of seed dispersal (Chambers and MacMahon 1994; Schupp and Fuentes 1995), distribution of open or protected space (McAuliffe 1988; Schupp 1995; Miriti et al. 1998), and longevity of seeds in the soil (Venable 1989).

Despite these and other studies, large gaps remain in our knowledge of seedling behavior in the arid Southwest. Field studies of seedling recruitment have, with some notable exceptions (e.g., Shreve (1917); Ackerman (1979), Miriti et al. (1998)), been limited in duration or scope. Moreover, basic life-history information (age-specific fecundity, seed mass, seedling survivorship, age at reproductive maturity, life span, presence or absence of a persistent seed bank) has yet to be collected for most perennial species. Such information is useful in both practical and theoretical contexts, such as predicting the response of plant populations to environmental variability or investigating constraints on life-history evolution.

Here we report on a six-year study of seedling emergence and survival at an ungrazed site in the northern Sonoran Desert. This site, the Desert Laboratory on Tumamoc Hill, Tucson, Arizona, was the location for earlier studies of seedling survival and emergence (Shreve 1911, 1917; Bowers 1994; Bow-

ers and Turner 2002) and for long-term studies of population dynamics (Goldberg and Turner 1986). For each species of interest, we obtained information about the amount of rain required for seedlings to emerge, season and frequency of emergence, seedling abundance, and survival in the years after emergence. In addition, we examined seedling survival as a function of rainfall, predation, and crowding. Finally, given evidence that life-history strategies encompass the seed and seedling stage, as in the correlation between seed size and life span (Silvertown 1981), for example, or the relative contribution of seedling recruitment to fitness of woody plants and herbaceous perennials (e.g., Silvertown et al. (1993)), we looked for distinctive patterns of emergence and survivorship in short-, moderate-, and long-lived species.

Methods

Study site

Tumamoc Hill (32°13′ N, 111°05′ W) is an outlier of the Tucson Mountains, Pima County, Arizona, USA. The study site encompasses about 352 ha and includes Tumamoc Hill proper, a rocky, basaltic-andesitic knoll (760 to 948 m above sea level), and the level or gently rolling plain to the west (725 to 760 m above sea level). Vegetation of the study site is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve and Wiggins 1964; Goldberg and Turner 1986). Dominants include *Cercidium microphyllum* (Torr.) Rose & Johnston, *Carnegiea gigantea* (Engelm.) Britt. & Rose, *Larrea tridentata* (Sess. & Moc. *ex* DC.) Coville, *Fouquieria splendens* Engelm., *Ambrosia deltoidea* (Torr.) Payne, *Encelia farinosa* A. Gray, *Aloysia wrightii* Heller *ex* Abrams, *Opuntia engelmannii* Salm-Dyck, *Acacia constricta* Benth., and *Ferocactus wislizeni* (Engelm.) Britt. & Rose. Nomenclature follows Kartesz (1994) with the exception of *Cercidium*. The study site has been protected from grazing by domestic livestock since 1907. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter-early spring (November to March), an arid late spring (April to June), a predictable summer monsoon (July to August), and a highly variable autumn (September to October). Maximum temperatures in summer often exceed 40 °C. Winters are generally mild, with occasional freezing temperatures. The period of study encompassed a hydrological drought associated with a La Niña episode in 1989 and a prolonged wet spell linked to El Niño conditions from 1991 to 1993.

Data collection

From August 1987 to September 1993, we studied seedling emergence and survival of perennial species on Area A, a 557-m^2 permanent vegetation plot on the rocky, north-facing slope of Tumamoc Hill. The plot, a parallelogram approximately 31 × 18 m, was established in 1910 for monitoring seedling survival (Shreve 1911, 1917). After substantial rains, we visited the plot to look for recently emerged seedlings. We marked all new seedlings with uniquely numbered aluminum tags, which we anchored to the ground with nails. At irregular intervals we visited the plot to record which seedlings had died and to remove their tags. In 1993, the final year, we checked for dead seedlings but did not mark any new ones. Because of time constraints, we recorded new seedlings of *Argythamnia neomexicana* Muell.-Arg., *Marina parryi* (Torr. & A. Gray) Barneby, *Sphaeralcea laxa* Woot. & Standl., and *Senna covesii* (A. Gray) Irwin & Barneby only during the first 1 or 2 years of the study. We recorded emergence pulses of the remaining species for the full 6 years. Here we report on emergence and survival of the 15 most abundant species.

Data analysis

Seasonal patterns in emergence
In the arid southwestern United States, the amount of rain needed to trigger germination of perennials ranges from 16 to 51 mm (Went and Westergaard 1949; Sherbrooke 1977; Steenbergh and Lowe 1977; Ackerman 1979; Bowers 1994; Bowers and Pierson 2001). Using this range as a guide, we examined the rainfall record in the weeks before each emergence event to determine which rainstorm likely triggered each pulse of germination. Because our censuses sometimes followed germination and emergence by several weeks or longer, we could not be absolutely certain in every case which storm was responsible. The smallest amount of rain in this study that resulted in germination and emergence of a given species was considered to be the minimum germinating rain for that species.

Spatial patterns in emergence
After each emergence event in 1987, 1988, and 1989, we used an electronic distance meter to determine the

location of all new seedlings. Coordinate locations were plotted for those species that were abundant enough for statistical analysis. Using geospatial software, the resulting plot maps were electronically gridded into 2-m² subplots and the number of seedlings in each determined. Morisita's index of dispersion (Morisita 1959) was calculated using the number of seedlings in quadrats of 2^x m² where x ranged from 1 through 8. Because Area A is a parallelogram, the 2-m² subplots on its perimeter were bisected by the sloping sides. These partial subplots were excluded from the Morisita analysis; only the central portion of the parallelogram, an 8 × 16 array of entire subplots, was used. Separate indices were calculated for each mapped species in all three years. Morisita's index is > 1 when seedlings are clumped, < 1 when seedlings are regularly dispersed.

Patterns of survival

We prepared tables of annual cohort survivorship for individual species and for the seedling population as a whole by counting the number of new seedlings in each year, then determining how many survived in each of the following years. Seedling survival, *S*, was calculated as:

$$S = N_{t+n} \div N_t,$$

where N_t = number of new seedlings at time t and N_{t+n} = number alive one, two, three, or four years later. (No seedlings survived beyond four years.) There were at least three potential sources of error in our estimates of survival: (1) we lost track of some seedlings because their tags were removed by animals, (2) some seedlings in every cohort doubtless died before we tagged and numbered them, and, (3) because of our irregular sampling schedule, the period from time t to time $t + n$ sometimes exceeded n years by one to several months.

Species longevity (Table 1) was determined from literature (Goldberg and Turner 1986) and personal observation, then seedlings were categorized as belonging to short-lived species (≤ 10 years), moderate-lived species (30 to 50 yrs), and long-lived species (≥ 75 years). The Survival Analysis module in SYSTAT (1998) was used to calculate survival probabilities within each longevity group on the basis of seedling life span. Due to our irregular sampling regime, the exact life span of any particular seedling was not known. The lower bound for life span in days was determined by subtracting the date when a seed-

ling was first observed from the date when it was last observed. The upper bound was calculated as the difference between the date when a seedling was first observed and the date when it was first recorded as absent. Given the upper and lower bounds of life span for a seedling, the Survival module (SYSTAT 1998) estimated where, in that interval, the probability of death occurred, then, from the proportion of seedlings failing at that point, calculated the survival probability.

We assessed causes of seedling mortality for the 1987 cohort by categorizing tagged seedlings as: (1) alive, (2) dead and desiccated, (3) dead and chewed, (4) dead and uprooted, and (5) tag found but seedling gone. These assessments were made in the last four months of 1987 and in March 1988.

We used logistic regression to evaluate the influence of rain on seedling survival. This statistical technique is appropriate when the dependent variable is categorical and binomial, and can be used with continuous and categorical independent variables (Trexler and Travis 1993). Logistic regression produces several statistics, including an odds ratio and a log likelihood. The odds ratio can be defined as "the multiplicative factor by which the odds change when the independent variable increases by one unit" (SYSTAT 1998:535). The log likelihood ratio relates the likelihoods of paired outcomes (living versus dead, for example) when the value of the independent variable is increased by one unit. Deviance (*D*), given by

$$D = -2\ln(\text{likelihood ratio})$$

expresses the size of the log likelihood ratio relative to a chi-square distribution (Trexler and Travis 1993).

We performed three separate logit analyses using rainfall (cm) in a specified period after germination as the independent variable and seedling status (alive or dead) after a specified period as the binomial dependent variable. Periods and sample sizes were as follows: first month after germination, N = 3728 (all seedlings in the data set); second through sixth months after germination, N = 1291 (those seedlings that survived at least 1 month); and seventh through twelfth months after germination, N = 621 (those seedlings that survived at least 6 months).

Finally, using the 2-m² subplots described above, we assessed the effect of crowding on seedling survival of *Ambrosia*, *Cercidium*, and *Larrea* in the years when they were relatively numerous. For each species and year we determined the proportion of seed-

Table 1. Life history and germination characteristics for 15 perennial species, 1987 to 1992. Observations were made on a 557-m^2 plot at Tumamoc Hill, Arizona, USA. Minimum rainfall = smallest amount of rain in this study that brought about germination. Ratio = emergence events:years of observation.

	Habit	Lifespan (yrs)	Minimum rainfall (mm)	Ratio	Month of emergence
Species					
Acacia constricta	Shrub	> 100	23.6	4:6	Jul, Aug
Ambrosia deltoidea	Shrub	50	23.9	4:6	Sep, Oct, Feb
Argythamnia neomexicana	Herb	5	17.5	4:2	Aug, Sep, Oct
Brickellia coulteri	Shrub	40	35.6	2:6	Aug
Cercidium microphyllum	Tree	> 100	17.5	12:6	Jul, Aug, Sep, Oct
Encelia farinosa	Shrub	30	35.6	3:6	Oct
Fouquieria splendens	Shrub	75	18.0	5:6	Mar, Jul, Aug, Oct
Janusia gracilis	Shrub	75	17.5	2:6	Sep, Oct
Jatropha cardiophylla	Shrub	75	–	1:6	Aug
Larrea tridentata	Shrub	> 100	17.5	9:6	Jul, Aug, Sep, Oct
Marina parryi	Herb	5	17.5	4:2	Aug, Sep, Oct
Psilostrophe cooperi	Herb	10	18.0	2:6	Mar, Aug
Senna covesii	Herb	10	18.8	3:1	Aug, Sep
Sphaeralcea laxa	Herb	5	17.5	4:2	Sep, Oct
Trixis californica	Shrub	40	18.0	2:6	Mar, Aug

lings in each subplot that died within 30 days of emergence, then plotted mortality as a function of density. To obtain a large sample for analysis, species and years were pooled, then nonlinear regression was used to describe the relation between the number of seedlings that emerged in each subplot and the proportion that died.

Results

Seasonal patterns in emergence

Altogether, more than 4300 seedlings were tagged; our analysis of 15 species comprised 3728 seedlings. Two distinct germination seasons could be discerned: early spring (February and March) and summer (July to October). More species emerged in August and October than in any other month (Table 1). Of 18 emergence events, four occurred in July, seven in August, two in September, three in October, and one each in February and March. Delays in the beginning of the summer rainy season probably account for the low frequency of emergence events in July and their high frequency in August. October germinations can be ascribed to unseasonal rains that were most likely from dissipating tropical cyclones. Germination was not expected in April to June, typically the driest time of year, and none was observed. The lack of germi-

nation between November and January was unexpected and might have reflected vagaries of seed supply more than climate. The minimum rain required for germination varied among species and ranged overall from 17.5 mm to 35.6 mm (Table 1).

Few species emerged in every year (Table 1). Seedlings of *Psilostrophe cooperi* (A. Gray) Greene, *Trixis californica* Kellogg, *Janusia gracilis* A. Gray, and *Brickellia coulteri* A. Gray, for example, were seen only twice in six years. *Jatropha cardiophylla* (Torr.) Muell.-Arg. emerged only once. Just two species, *Cercidium microphyllum* and *Larrea tridentata*, appeared annually. The largest *Larrea* cohorts (N = 105, N = 237) emerged in October; small numbers of seedlings germinated in other months, as well (July, N = 3; August, N = 13; September, N = 2, N = 6). Other woody species that tended to emerge in relatively large numbers included *Ambrosia deltoidea*, *Cercidium*, *Encelia farinosa*, and *Trixis* (Figure 1). Annual cohorts of the remaining woody species were small (< 20 individuals). Among herbaceous perennials, *Argythamnia*, *Marina*, and *Sphaeralcea* also produced large cohorts (Figure 1). Long-lived species apparently had more opportunities for germination than moderate-lived species (Figure 2).

Not shown in Table 1 are species that appeared rarely or in very small numbers: *Abutilon incanum* (Link.) Sweet, *Allionia incarnata* L., *Baccharis sarothroides* A. Gray, *Ferocactus wislizeni*, *Gutierrezia*
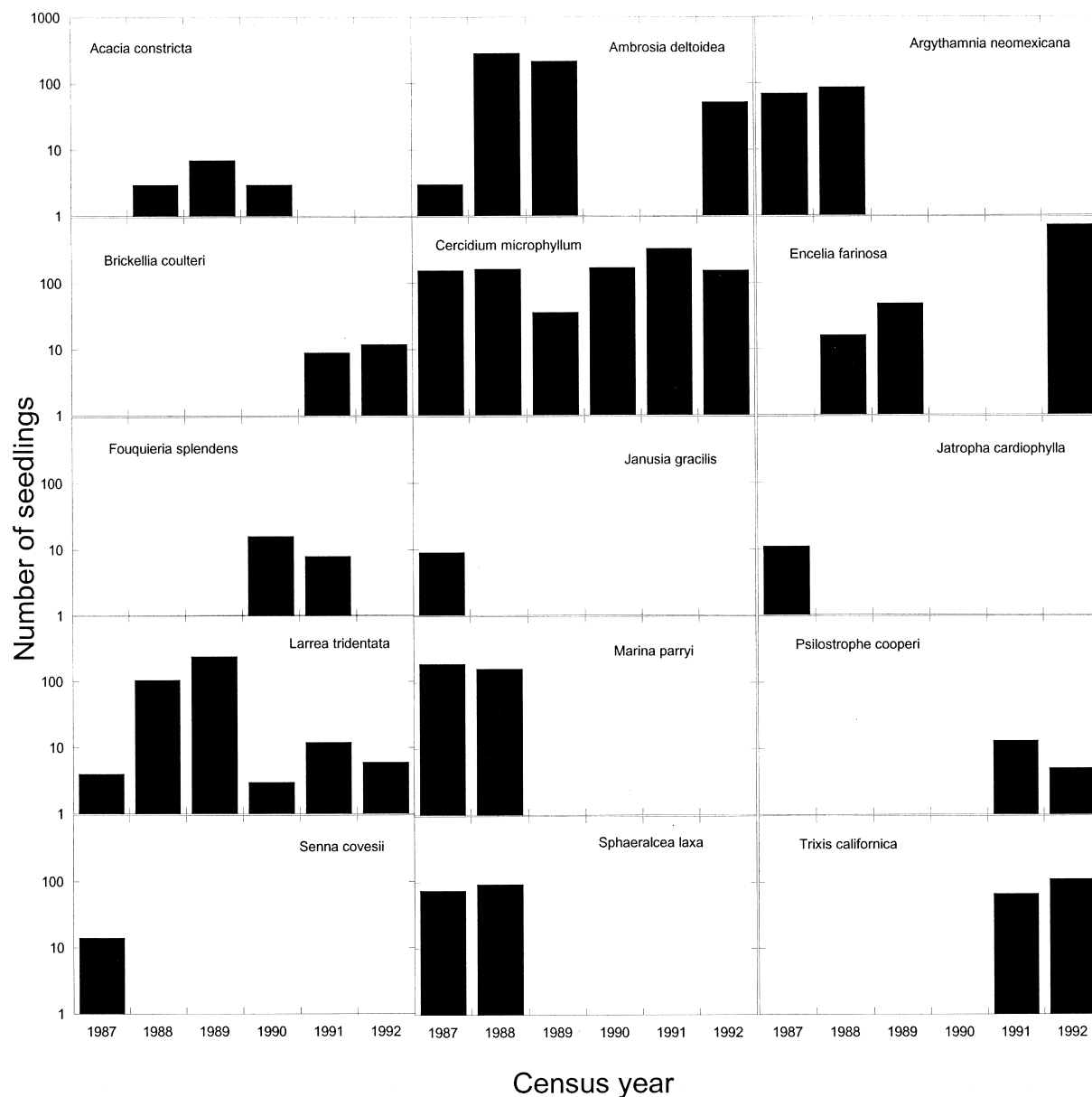
Figure 1. Size of annual cohorts for 15 species of perennial plants on a 557-m^2 plot at Tumamoc Hill, Arizona, USA. Years without bars indicate years without emergence except for *Argythamnia, Marina, Senna,* and *Sphaeralcea,* new seedlings of which were not monitored after 1988.

sp., *Hibiscus denudatus* Benth., *Menodora scabra* A. Gray, *Opuntia* spp., *Pennisetum ciliare* (L.) Link., and *Prosopis velutina* Woot. Although adult plants of *Carnegiea gigantea* and *Lycium berlandieri* Dunal were not uncommon on the plot, we found no recently germinated seedlings of either species. Seedlings of *Ayenia microphylla* A. Gray and *A. compacta* Rose were sometimes abundant, but we could not identify them

to species with confidence and did not include them in our analyses.

Spatial patterns in emergence

Spatial patterns of emergence were examined for *Ambrosia deltoidea, Cercidium microphyllum,* and *Larrea tridentata.* Newly emerged seedlings of *Ambrosia* and *Larrea* were clumped, whereas those of *Cercid-*
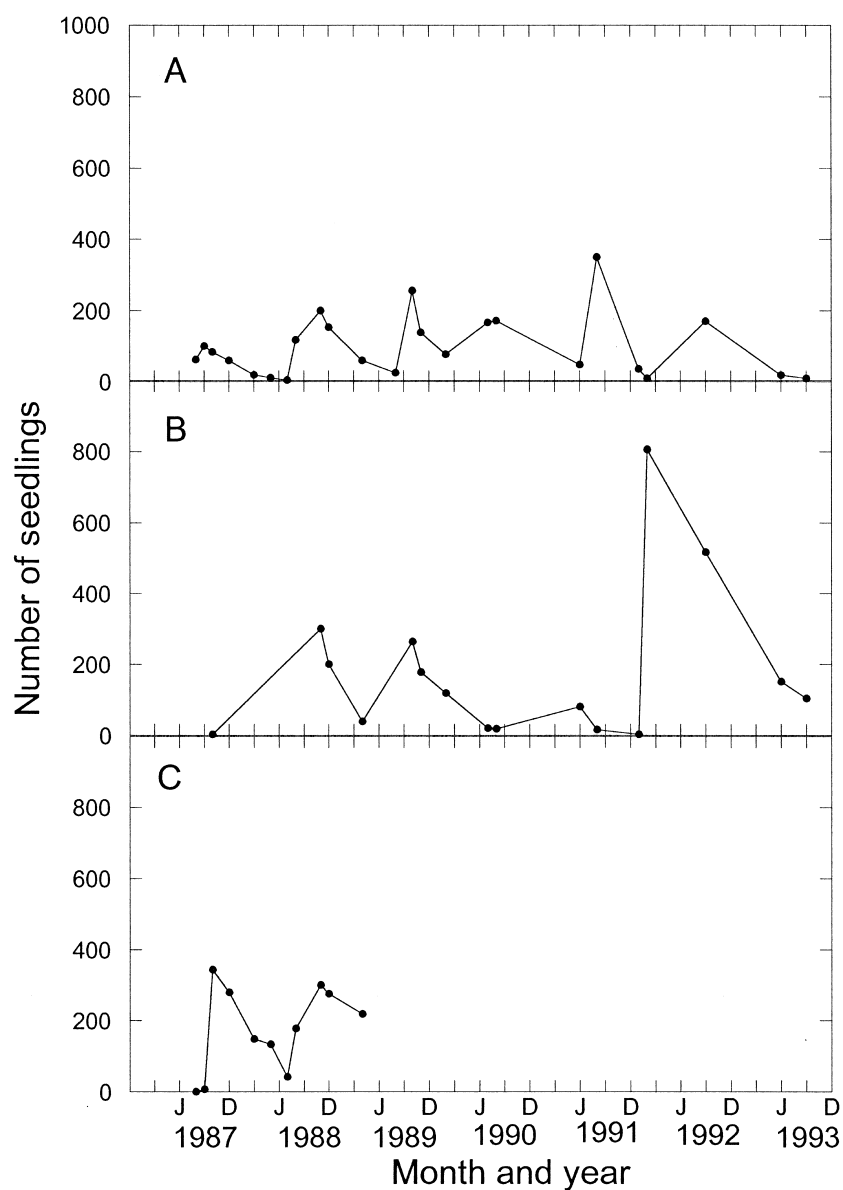
Figure 2. Total population of seedlings of perennial plants on 25 observation dates from 1987 to 1993. Observations were made on a 557-m² plot at Tumamoc Hill, Arizona, USA. (A) long-lived species (N = 6), (B) moderate-lived species (N = 4), (C) short-lived species (N = 5). Total population of short-lived species is shown only for the first two years of the study because new seedlings of *Argythamnia*, *Marina*, *Senna*, and *Sphaeralcea* were not monitored after 1988.

ium were scattered (Figure 3). For *Ambrosia* and *Larrea*, Morisita's index was relatively high at small spatial scales, indicating aggregation, and close to 1 at the largest scales, indicating that clumps were randomly distributed within the plot (Figure 4). In contrast, the index for *Cercidium* was close to 1 at all spatial scales, showing that dispersion was random (Figure 4).

Patterns of survivorship

The number of seedlings in a cohort generally declined rapidly during the first year (Table 2). Few seedlings lived longer than two years (Table 2). Within individual species, first-year survival ranged from 0.0% to 18.1% (an unusually high rate), second-year survival from 0.0 to 5.3%, and third- and fourth-year survival from 0.0 to 0.3% (Table 3). Note that
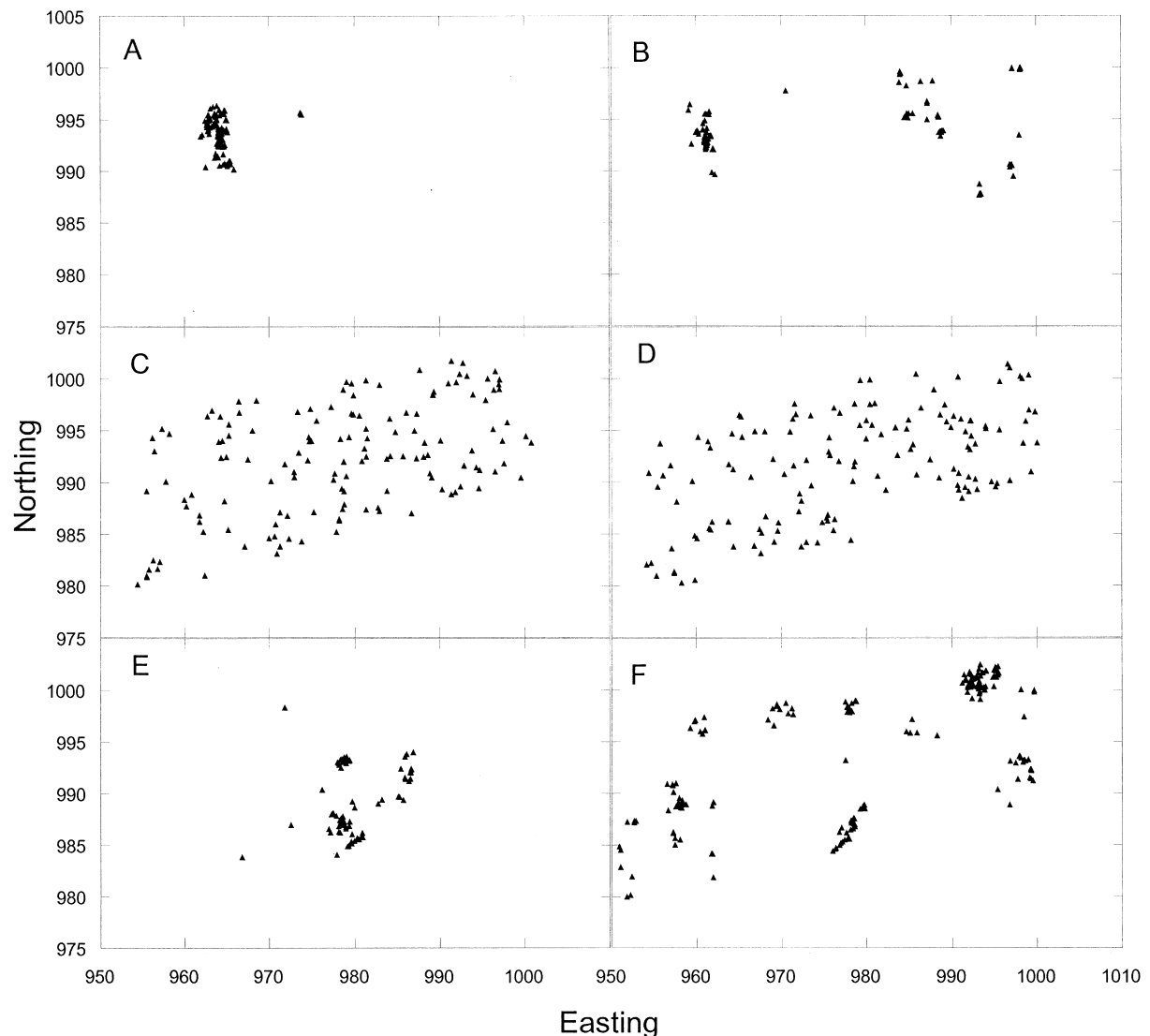
Figure 3. Location of seedlings of selected species on a 557-m² plot at Tumamoc Hill, Arizona, USA. (A) *Ambrosia deltoidea*, 1988, (B) *A. deltoidea*, 1989, (C) *Cercidium microphyllum*, 1987, (D) *C. microphyllum*, 1988, (E) *Larrea tridentata*, 1988, (F) *L. tridentata*, 1989.

survival values in Table 3 are not averages; rather, they represent the total number of seedlings tagged during the study and the proportion of them that survived in the following years.

Survival probabilities appeared to be correlated with species longevity. Survivorship of long-lived species declined steeply at the start and remained lower than that of short- or moderate-lived species (Figure 5). At first, short-lived species showed much better survival than long- or moderate-lived species (Figure 5). After about 300 days, however, survival of moderate-lived species exceeded that of short-lived species (Figure 5).

Four species in the 1987 cohort were abundant enough for us to calculate the proportion that died from different causes. Seedlings described as "tag found but seedling gone," "dead and chewed," or "dead and uprooted" were assumed to have succumbed to predation. On average, 37.4% of seedlings died from predation, whereas only 12.9% died from desiccation, a significant difference ($t = 3.01$, $P < 0.05$).

In logistic regression, increased rain in the first month had essentially no effect on seedling survival (odds ratio = 1.0; $D = 3.94$, $P = 0.05$). Possibly the rain required for gemination and emergence is enough
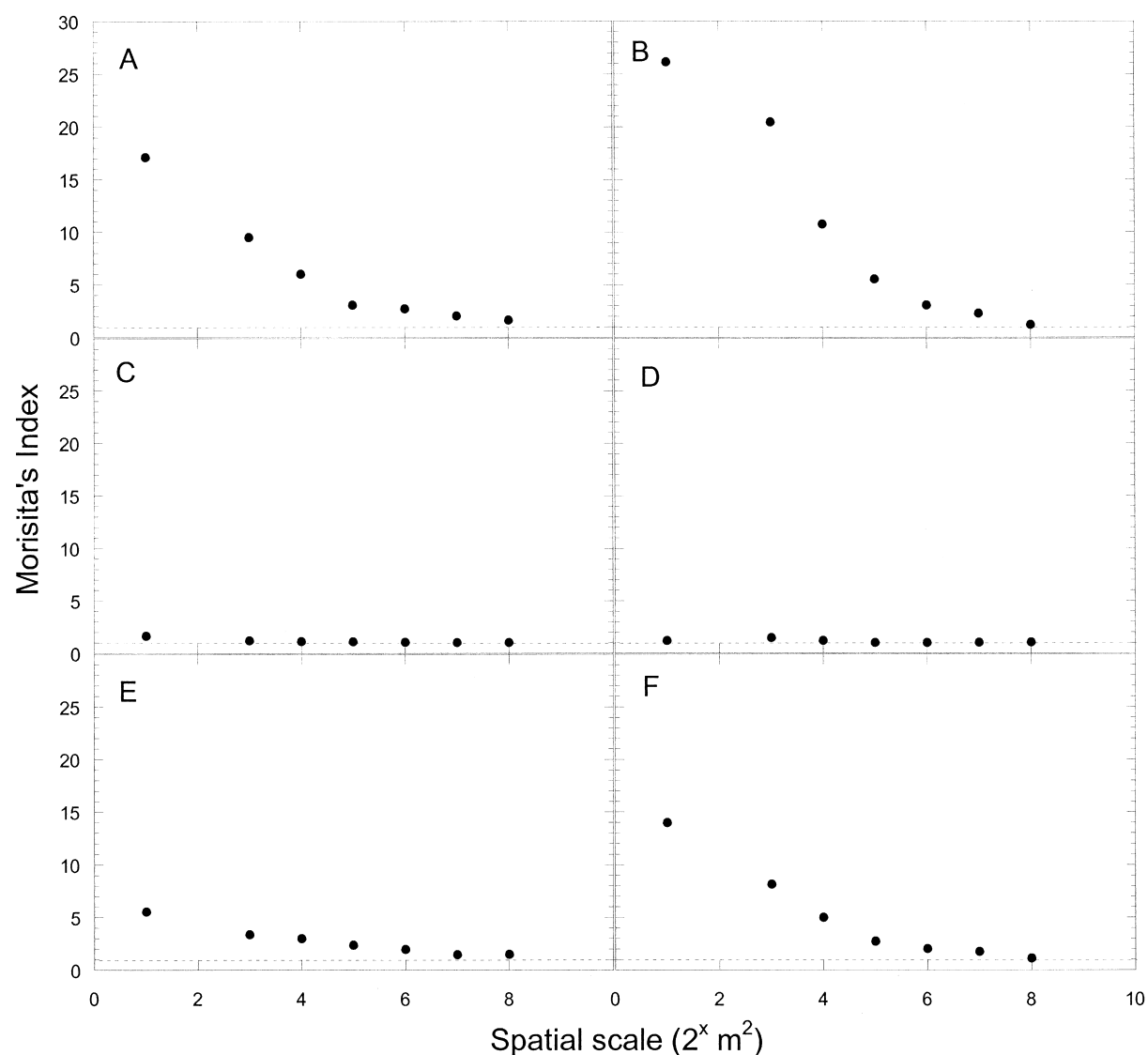
Figure 4. Morisita's index of dispersion for seedlings of selected species on a 557-m^2 plot at Tumamoc Hill, Arizona, USA. (A) *Ambrosia deltoidea*, 1988, (B) *A. deltoidea*, 1989, (C) *Cercidium microphyllum*, 1987, (D) *C. microphyllum*, 1988, (E) *Larrea tridentata*, 1988, (F) *L. tridentata*, 1989. Morisita's index is > 1 when seedlings are clumped, < 1 when seedlings are regularly dispersed.

to keep seedlings alive for the first month; if so, one would not expect additional moisture to improve survival. From the second to sixth months after germination, rain had a marked effect on seedling survival ($D = 687.59$, $P < 0.001$); an increase of 1 cm in rain improved the odds of survival by a factor of 1.4. In the seventh through the twelfth months, a 1-cm increase in rain improved the odds of survival only slightly (odds ratio = 1.1). Despite the low odds, the sizable log likelihood ratio ($D = 80.64$, $P < 0.001$) indicates that survival increased with rain even after the first six months.

The analysis of crowding and seedling mortality provided no strong evidence for density-dependent mortality. Many subplots experienced 100% mortality regardless of initial seedling density (Figure 6). In the pooled data set, there was no relation between mortality and density ($r^2 = 0.01$).

Discussion

During 6 years of observation, more than 3700 seedlings of 15 perennial plant species were recorded on

Table 2. Survivorship of annual cohorts from 1987 to 1993 on a 557-m² plot at Tumamoc Hill, Arizona, USA. Annual cohorts are comprised of all seedlings that germinated in the same year. Values show how many seedlings from each cohort survived at least 12 months. Existing seedlings were monitored in 1993 but no new ones were marked. Values represent pooled seedlings (N = 3728) of 15 species of perennial plants.

| | Census year | | | | | | |
	1987	1988	1989	1990	1991	1992	1993
Cohort							
1987	535	29	1	1	0	0	0
1988		921	9	1	0	0	0
1989			552	21	5	4	2
1990				196	7	1	0
1991					431	7	1
1992						1093	140
Total	535	950	562	219	443	1105	143

a 557-m² plot. Only 2 of 2008 seedlings tagged between 1987 and 1989 survived as long as 4 years (0.1%) (Table 2), somewhat lower than in the Mojave Desert, where 1 of 201 seedlings survived that long (0.5%) (Ackerman 1979). First-year survival averaged across all species was similar in the two studies: 3.7% in our study, 3.3% in the Mojave Desert (Ackerman 1979).

The timing of emergence in our study was highly variable (Table 1). A few species emerged several times in a single year; others appeared only once or twice in the six years of the study (Figure 1). Frequency of emergence depends in part on frequency of adequate rains at temperatures suitable for germination (Beatley 1974; Boyd and Brum 1983a; Bowers 1994). Because large storms occur less frequently than small ones (Shreve 1914), species with high moisture requirements for germination are not likely to emerge annually. The minimum rain required for germination and emergence varied according to species and ranged from 17.5 to 35.6 mm. In some years, despite ample seasonal rains, no seedlings of *Brickellia coulteri*, *Encelia farinosa*, *Fouqieria splendens*, *Jatropha cardiophylla*, *Janusia gracilis*, or *Trixis californica* were observed. Flower production and seed set of these species can be highly variable from year to year, as can level of seed predation, and we suspect that in some years there were few or no seeds in the soil when germinating rains occurred.

Episodic germination doubtless reflects the variable occurrence of different types of storms. Many species germinate during summer rains (Table 1), thus taking advantage of a predictable climatic phenomenon. Since about 1976, however, the summer monsoon has become increasingly erratic (Swetnam and Betancourt 1998), and, as a result, the delay between seed dispersal and germination has increased, leaving seeds at greater risk of predation (Bowers 1994). Other species apparently depend on unpredictable seasonal rains for germination; these include *Agave deserti* Engelm., *Fouquiera splendens*, *Larrea tridentata*, and *Prosopis* spp. (Jordan and Nobel 1979; Rivera and Freeman 1979; Turner 1990; Bowers 1994). In the case of *Larrea tridentata*, mass germination has been reported following heavy rains in September (Sheps 1973; Beatley 1974; Rivera and Freeman 1979; Zedler 1980), which is usually a dry month; we found large numbers of *Larrea* seedlings in October, which is typically dry as well. Storms that trigger germination in late September and October are often dissipating tropical cyclones that bring large amounts of rain to a relatively broad area, sometimes over several consecutive days. The importance of this type of storm to the ecology of Sonoran Desert plants has perhaps not been adequately recognized. Because of their wide coverage, tropical cyclones might result in spatial autocorrelation of germination across the desert region, especially for species that rely heavily on autumn rainfall (*Larrea tridentata*, for example). Summer convective storms, which are local in their effects, are more likely to produce local cohorts that are not coordinated spatially. On the other hand, convective storms bring enough rain for germination of certain species virtually every year (e.g., *Cercidium microphyllum*), whereas tropical cyclones are infrequent in southern Arizona (Webb and Betancourt 1992).

Variability in the regeneration niche also reflects climatic variation on larger scales, particularly large-scale interactions between the atmosphere and the ocean. El Niño-Southern Oscillation (ENSO) conditions prevail about every three to seven years (Webb and Betancourt 1992), and the Pacific Decadal Oscillation (PDO) fluctuates over 10 to 20 years (McCabe and Dettinger 1999). By influencing frequency and type of storm, ENSO and PDO contribute to variability in the regeneration niche. During El Niño years, for example, tropical cyclones are more likely to reach the southwestern United States (Webb and Betancourt 1992), and heavy precipitation events in winter are more frequent (Cayan et al. 1999). Conversely, La Niña years are associated with unusually dry winters and somewhat wetter summers (Kahya and Dra-

Table 3. Seedling survival and lifespan for 15 perennial plant species on a 557-m^2 plot at Tumamoc Hill, Arizona, USA. Survival values represent the proportion of tagged seedlings that survived for 1, 2, 3, or 4 years.

|	Number tagged	Percent surviving				Mean lifespan (days)	
		1 yr	2 yr	3 yr	4 yr	Lower bound	Upper bound
Species							
Acacia constricta	12	0.0	0.0	0.0	0.0	96.9	205.7
Ambrosia deltoidea	564	1.2	0.2	0.2	0.2	44.8	143.6
Argythamnia neomexicana	155	6.5	0.7	0.0	0.0	155.8	252.1
Brickellia coulteri	21	0.0	0.0	0.0	0.0	17.5	207.2
Cercidium microphyllum	1008	1.2	0.1	0.1	0.0	44.0	189.8
Encelia farinosa	816	18.1	0.3	0.3	0.1	148.4	299.7
Fouquieria splendens	18	5.6	0.0	0.0	0.0	41.9	254.7
Jatropha cardiophylla	11	0.0	0.0	0.0	0.0	25.0	52.2
Janusia gracilis	9	0.0	0.0	0.0	0.0	49.8	111.9
Larrea tridentata	384	1.6	0.5	0.3	0.3	56.5	138.7
Marina parryi	345	5.8	0.3	0.3	0.0	128.7	216.0
Psilostrophe cooperi	19	5.3	5.3	0.0	0.0	70.1	134.1
Senna covesii	20	5.0	0.0	0.0	0.0	67.6	140.8
Sphaeralcea laxa	169	4.1	0.0	0.0	0.0	148.4	240.3
Trixis californica	177	0.0	0.0	0.0	0.0	16.0	187.0
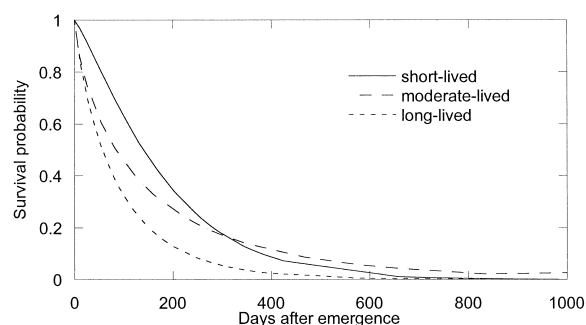
Figure 5. Survival probability for seedlings of perennial plants on a 557-m^2 plot at Tumamoc Hill, Arizona, USA. Seedlings grouped by life span as follows: short-lived, N = 5 species; moderate-lived, N = 4 species; long-lived, N = 6 species.

cup 1994). Winter precipitation in the southwestern United States is also correlated with PDO; in addition, PDO conditions can strengthen the climatic effects of ENSO (McCabe and Dettinger 1999).

Rain is obviously necessary for germination and survival throughout the first year of life, and in our study there was a strong tendency for survival to increase with rain. Unusually high first-year survival (18.7%) of an *Encelia* cohort that emerged in February 1992 was probably related to high rainfall (615 mm) in the following twelve months, including 45 mm of rain during the normally hot, dry months of April and May. On the other hand, a cohort of *Ambrosia* seedlings emerging at the same time experi-

enced 98% mortality in the first year despite the plentiful rain. Clearly, the beneficial effects of rain can be overwhelmed by other factors (McAuliffe 1986; Miriti et al. 1998).

One such factor is predation. Our limited data suggest that many seedlings were eaten before they had a chance to die from drought (see also Owens and Norton (1992)). In other studies, as well, herbivores accounted for a large proportion of seedling mortality among Sonoran desert dominants such as *Larrea tridentata*, *Cercidium microphyllum*, and *Carnegiea gigantea* (Sheps 1973; Boyd and Brum 1983a; McAuliffe 1986; Steenbergh and Lowe 1977). In particular, seedlings of *C. microphyllum* showed little sign of drought stress during a prolonged drought but succumbed in large numbers to predation (McAuliffe 1986).

Another potential hazard is crowding, which can lead to competition for resources and also can increase the risks of infection by pathogens and consumption by herbivores (Howe and Smallwood 1982; Augspurger and Kelly 1984). We did not find any correlation between early mortality of *Ambrosia*, *Cercidium*, or *Larrea* and seedling density in 2-m^2 subplots. Other studies of desert plants similarly have found no relation between crowding and seedling survival (Ebert and McMaster (1981) and Hunter (1989); but see Owens and Norton (1989)). Competition (or at least proximity) between seedlings and adults,
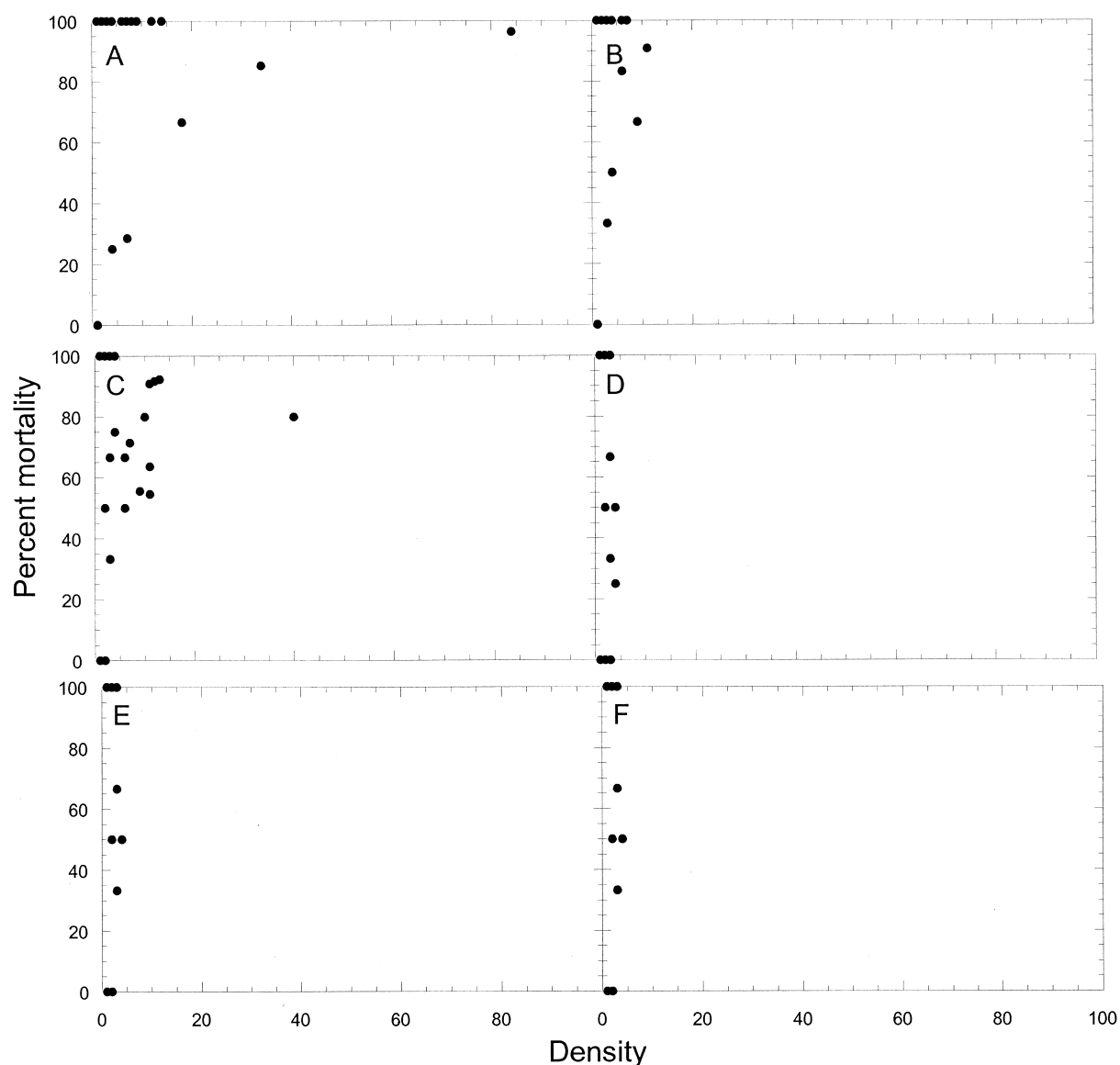
Figure 6. Seedling mortality within 30 days of emergence as a function of density in 2-m² subplots. Observations were made on a 557-m² plot at Tumamoc Hill, Arizona, USA. (A) *Ambrosia deltoidea*, 1988, (B) *A. deltoidea*, 1989, (C) *Cercidium microphyllum*, 1987, (D) *C. microphyllum*, 1988, (E) *Larrea tridentata*, 1988, (F) *L. tridentata*, 1989.

however, can be a large factor in seedling mortality of *Larrea* (Sheps 1973; Boyd and Brum 1983a) and *Ambrosia dumosa* (A. Gray) Payne (Hunter 1989). Seeds of *Larrea* tend to be concentrated under canopies of parent plants (Barbour et al. 1977; Rivera and Freeman 1979), and the same is true of *Ambrosia deltoidea* (pers. obsv.). In our study, mortality of *Ambrosia* and *Larrea* seedlings might have been a function of proximity to adult plants; our data did not allow us to test this hypothesis, however.

Even at the seedling stage, short-, moderate-, and long-lived species displayed distinct life-history strategies. Short-lived species (*Argythamnia, Senna, Marina, Psilostrophe, Sphaeralcea*) had relatively high seedling survival. Because these species can bloom in their first or second year, good early survival meant that some individuals were able to reproduce before they died. Moderate-lived species (*Ambrosia, Brickellia, Encelia, Trixis*) exhibited highly episodic germination and emergence (Figures 1 and 2), a poten-

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tially risky behavior that might have been offset to some extent by relatively good long-term survival. Long-lived species (*Acacia, Cercidium, Janusia, Jatropha, Larrea*) perhaps compensated for generally poor seedling survival by frequent germination and emergence.

Our results affirm that seedling establishment in arid environments is highly episodic. For that reason, only long-term studies can provide reliable estimates of annual survivorship and indicate actual frequencies of establishment. Given the results shown in Tables 2 and 3, we doubt that a 6-year study is long enough. We also wonder whether our results might reflect to some extent the limited spatial scale of our study. Because the total number of seedlings sampled is also a function of spatial scale, at least in part, enlarging the scale to increase cohort size by an order of magnitude might improve the odds of finding survivors after a year or two.

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